

Modelling frugivore-mediated seed dispersal

by

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Declaration

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Abstract

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Seed dispersal is the movement of seeds away from parent plants, and is a crucial ecological process for plant reproduction, persistence and spatial distribution. Specific interest in frugivorous seed-dispersal has increased due to its importance for plant temporal and spatial dynamics under global change. Empirical studies confirm that the interaction between fleshy-fruited plants and frugivores is mutualistic and can be fully beneficial for both partners provided that the dispersal cost is low. The animals benefit is quite obvious (food) while plants benefit is seed dispersal leading to reduced level of plant aggregation among other benefits. Based on pair-approximation method, we here propose a process-based mechanistic model of frugivorous seed-dispersal that captures the dynamics of the global and local densities of plants and the density of frugivores. The model considers three essential components of frugivorous seed-dispersal, including the strength of plant-frugivore mutualistic interaction, dispersal efficiency of frugivores and germination probability of seeds. Our theoretical findings agree with previous empirical studies that seed dispersal decreases plant intraspecific competitions by reducing the level of plant clustering. Results show that efficient frugivorous animals allow conditional persistence of plants with low fecundity and natural dispersal ability. Otherwise, inefficient animal seed-dispersers, with high dispersal risks, will act as seed predators, leading to global extinction of plants. Finally, results show the animals benefit (increased density equilibrium of animals) from plant-frugivore mutualistic interaction. Interestingly, our results provide broad theoretical evidence for the paramount importance of the existence of frugivore species in tropical forests.

Highlights

Based on our theoretical findings from frugivorous seed-dispersal model, together with the information gathered during this project, the following claims are being set to complement empirical studies of seed dispersal:

- Frugivorous seed-dispersal is a crucial ecological process for plant persistence, spatial distribution, forest restoration and ecosystem functioning.
- Efficient animal seed-dispersers extend and allow conditional persistence of plants in otherwise poor habitat that requires high plant fecundity and dispersal rates. Thus, frugivorous seed-dispersal can be an efficient strategy for plants to escape extinction.
- Frugivorous seed-dispersal decreases plant intraspecific competition by reducing the level of plant aggregation.
- Inefficient animal seed-dispersers can act as the main drivers of plant extinction if the dispersal cost is high. Loss of frugivore species in tropical regions may also drive tropical plants to extinction.
- Plant spatial distribution largely depends on the spatial distribution of the dispersal agents. The spatial distribution of plants can be imprinted by frugivore spatial distribution.
- Without frugivorous seed-dispersal, only plants with high fecundity and high local dispersal ability can be conserved.

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Dedications

*I dedicate this work to my mother, father, siblings and all who stayed
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Chapter 1

Introduction

This chapter provides a general review of seed dispersal and its mechanisms with focus on frugivorous seed-dispersal. It also gives a general idea of our frugivorous seed-dispersal model.

1.1 Seed dispersal: a review

Dispersal, defined as the unidirectional movement of organisms or dispersion of individuals away from their birthplaces, is a crucial process in plant movement ecology (Howe & Smallwood 1982, Willson & Traveset 2000, Traveset et al. 2013). It could have profound impact on plant community dynamics (Beckman & Rogers 2013), preserve plant biodiversity (Herrera 1989) and prevent them from extinction (Caughlin et al. 2015). Generally, dispersion of individuals determines the spatial distribution of species (Park et al. 1999, Nathan & Muller-Landau 2000), and is considered among the main ecological processes that shape population densities (Greenwood 1982). Not only can it determine the rate at which species spread (Nathan & Muller-Landau 2000, Levin et al. 2003) but also stabilizes population dynamics in fluctuating environments (Doebeli 1995, Kadmon 1997).

Seed dispersal is the movement of seeds away from the parent trees, and has been playing a crucial role in plant temporal and spatial dynamics, reproduction (Howe & Miriti 2004), persistence (Archer & Pyke 1991, Robledo-Arnuncio et al. 2014) and diversity conservation (Howe 1984, Herrera 1989 & 2002, Trakhtenbrot et al. 2005, Stoner & Henry 2009, Traveset et al. 2013). It can also have profound impacts on both spatial patterns of seedlings and plant spatial distribution (Nathan & Muller-Landau 2000, Beckman et al. 2012). Seedling and plant spatial distributions largely depend on their dispersal agents and how they disperse seeds in space (Seidler & Plotkin 2006, Nathan & Muller-Landau 2000). Plants can often find relatively suitable habitats for growth and survival by using dispersal vectors to disperse their propag-

ules away, and may colonize new geographical locations. Seed dispersal may not be sufficient for colonization, and plants must be able to resist biological hazards, survive and reproduce to establish new plant populations. However, if all seeds produced by a plant fall underneath the parent plant, then competition for resources such as light, water and nutrient limits seeds growth and establishment (Howe 1984). Established plants often deny to share resources within new neighboring seedlings, and such seedlings will most likely die. By transporting seeds far away, plants can reduce intraspecific competition, inbreeding pressure, fungal pathogens and lessening density-dependent seed mortality near the parental trees (Howe 1984, Herrera 2002). Empirical studies confirmed that the probability of seed establishment increases with increased distance between each two individual plants (Beckman & Rogers 2013), and as such can also be maximized by seed dispersal.

The significance of seed dispersal for plant reproduction and persistence clearly appears in tropical regions where many plants entirely rely on frugivores to disperse their seeds (Howe & Miriti 2004, Chama et al. 2013, Perez-Mendez et al. 2015). However, seeds can be dispersed by several dispersal vectors including animals, wind, water, gravity and human beings (Levin et al. 2003, Wichmann et al. 2009). The dispersal mechanism depends on several factors such as fruit quality and size as well as height of plants. For example, large fruits may fall down on the ground due to gravitational force or can be dispersed by large frugivores, and may not be dispersed by wind (Herrera 2002, Perez-Mendez et al. 2015). Relatively large seeds, heavier than 100 mg, can only be dispersed by vertebrates and relatively smaller seed can only be dispersed by wind (Herrera 2002). However, smaller seeds have a higher chance of being dispersed but they have a lower probability of being germinated and established (Alcantara & Rey 2003). Large fruits are usually eaten by mammals and smaller fruits are eaten by birds due to the differences in their gape limitation (Howe 1986, Jordano 2000, Herrera 2002, Alcantara & Rey 2003), leading to a strong seed dispersal limitation (Alcantara & Rey 2003, Perez-Mendez et al. 2015).

1.1.1 Dispersal Mechanisms

Plants have a very limited mobility and can not actively disperse their seeds around, thus often rely on dispersal vectors to act as seed carriers. Seeds can be dispersed in several ways (Willson 1993b). However, we briefly review the most common dispersal mechanisms, including seed dispersal by wind, water, gravity and animals. Indeed, the dispersal mechanism greatly depends on fruit morphology, height of plants as well as environmental conditions (e.g., in case of wind dispersal) where plants grow. This thesis focuses on frugivorous seed-dispersal, therefore this mechanism will receive most of our attention.

1.1.1.1 Wind-mediated dispersal

Some plants disperse their seeds away by using wind power (Herrera 2002). Seeds that are dispersed by wind have some special characteristics such as wings or fluff. Also, they are often small and light to allow themselves to be transported by wind. The spatial distribution of seeds dispersed by wind and the distance traveled by seeds are determined by both wind direction and speed (Jongejans & Telenius 2001, Soons et al. 2004).

1.1.1.2 Gravity-mediated dispersal

Fruits dispersed by gravity are often heavy and ripe and they fall down on the ground due to gravitational forces. Such fruits may also be dispersed by large frugivorous animals. Seeds dispersed by gravity can also allow dispersion of seeds by water or animals at later stages.

1.1.1.3 Water-mediated dispersal

Plants that grow inside the water or along streams often disperse their seeds away by using water. Seeds that are transported by water can travel long distances far away from the parent plants.

1.1.1.4 Animal-mediated dispersal

Frugivorous animals visit plants, consume their fruit pulps and the eaten seeds will not be digested and will be dropped out often away from the parent trees (Schleuning et al. 2011). Animal-mediated seed dispersal is referred to as endozoochory and is the most crucial dispersal mechanism in tropical ecosystems where plants rely on animal seed-disperser (Howe & Smallwood 1982). The most essential frugivore species that are responsible for seed dispersal in tropical regions are birds and mammals. Many empirical studies confirmed that frugivores disperse seeds away from parental plants. The interactions between plants and frugivore species have been observed widely and frugivores often spend time handling fruits (Schleuning et al. 2011). Large frugivores play an important role in the ecology of seed dispersal due to their ability of consuming large fruits and their effectiveness of dispersing large seeds (Perez-Mendez et al. 2015).

Efficient frugivore seed-dispersers can disperse large number of seeds to a suitable and less competitive environment where seed can germinate with relatively low probability risk (Bonte et al. 2012, Mokotjomela et al. 2016), as opposed to inefficient dispersers which might be seed predators that damage seeds (Janzen 1970, 1971). Frugivorous animals not only disperse seeds but may also enhance seeds germination by passing the seeds through their guts or depositing seeds into relatively better environmental conditions for survival

and growth (Calvino-Cancela 2004, Beckman & Rogers 2013). Caughlin et al. (2015) found that the loss or overhunting of frugivores in tropical regions increases the extinction risk of plants and decreases tree population viability. Frugivore-mediated seed dispersal can be affected by factors such as habitat fragmentation and heterogeneity (Brudvig et al. 2015).

1.2 Advantages and disadvantages of frugivorous seed-dispersal

Frugivorous seed-dispersal could be advantageous or disadvantageous for plant populations and communities (Janzen 1970, 1971, Bonte et al. 2012). However, it is often beneficial for plant species (Caughlin et al. 2015, Mokotjomela et al. 2016) and survival probability of seeds is more likely higher away from parental trees (Beckman & Rogers 2013). In addition to colonizing new geographical regions (Robledo-Arnuncio et al. 2014), seed dispersal benefits plants by providing them suitable habitats for survival and escaping unfavorable environmental conditions (Beckman & Rogers 2013). Empirical studies show the advantages of seed dispersal for plants, and suggests that at least 75% of the tropical trees require light gap in order to grow (Howe 1984). The interaction between fleshy-fruited plants and animals feeding on their fruits is of a mutualistic nature (Willson 1993a, Herrera 2002, Schleuning et al. 2011), and it is therefore beneficial for both partners. The indirect benefit for plants is seed dispersal which reduces the plants intraspecific competition for resources, inbreeding pressure, and lessens density-dependent seed mortality near the parent plants (Howe & Smallwood 1982, Herrera 2002, Robledo-Arnuncio et al. 2014). However, plant benefits from plant-frugivore mutualistic interaction differs among frugivore species themselves (Jordano et al. 2007). Empirical studies confirmed that small-sized birds are usually responsible for short-distances dispersal while both large-sized birds and mammals are responsible for long-distances dispersal (Jordano et al. 2007). Thus, the influence of frugivore-mediated seed dispersal on plant spatial and temporal dynamics varies and depends on types of frugivores dispersing plant seeds. However, plant-frugivore interactions and seed dispersal has been studied in a network and found that these interactions are beneficial for ecological restoration and ecosystem functions (da Silva et al. 2015). The direct benefit for animals is that the ingested fruits will be converted into the animals biomass, and so plants support animals by providing extra food resources.

Seed dispersal by fruit-eating animals might sometimes be disadvantageous for plants (Janzen 1970, Jordano 2000, Bonte et al. 2012) for the following reasons: (1) its success depends on the dispersal agents which may sometimes kill or crush the seed during ingestion, through digestion, and ejection (Janzen 1971,

Herrera 2002, Howe & Estabrook 1977 & 1984); (2) seed dispersal is sometimes risky for the plants (Bonte et al. 2012) and may drive plants to local extinction (Harada & Iwasa 1994, Caughlin et al. 2015); (3) Seeds, seedlings and plant spatial distribution is largely influenced by the spatial distribution of their dispersal agents (Nathan & Muller-Landau 2000). Considering the dispersal risk, only a fraction of the eaten seeds might be dispersed and deposited into suitable environmental conditions for germination and establishment. However, the fate of the dispersed seeds is rarely considered in the literature (Nathan & Muller-Landau 2000, Heleno et al. 2011). Our model considers dispersal costs associated with frugivorous seed-dispersal (Bonte et al. 2012).

1.3 Frugivore visitation

Plants encourage seed dispersers to visit and disperse their seeds (Herrera 2002) by developing attractive fruits to entice more visitors as well as to maximize the number of potential visits (Howe & Estabrook 1977). The number of animal visitations and the strength of plant-frugivore mutualistic interaction are influenced by elements such as fruits quality and the availability of other food resources (Jordano et al. 2007). Howe & Estabrook (1977) and Schleuning et al. (2011) have shown that the availability of fruits increases the number of visits by potential dispersers, and increases the probability of dispersing seeds. However, Jordano (2000) argues that the number of consumed fruits per visit depends on the body mass of frugivores.

1.4 Why frugivorous seed-dispersal matters?

Frugivorous seed-dispersal takes into account several factors such as the strength of plant-frugivore interaction, dispersal efficiency (Schupp 1993, Bonte et al. 2012, Mokotjomela et al. 2016) and availability of other food resources (Hampe 2008). The fate of eaten and dispersed seeds is not yet well-documented in the literature (Nathan & Muller-Landau 2000). However, in addition to financial cost it is also quite hard to track individual birds and mammals in order to count the consumed and dispersed seeds. Importantly, we need some mechanisms to measure the costs of frugivorous seed-dispersal and to predict the temporal and spatial dynamics of plants. One possible mechanism will be by proposing process-based mechanistic models to improve our understanding of plant-frugivore mutualistic interaction. This will provide us with insights on how our ecosystems behave when dispersers efficiency is varied. It is also crucial to understand the influence of frugivorous seed-dispersal on plant spatial distribution, persistence and ecosystem function (Nathan & Muller-Landau 2000, Cortes & Uriarte 2013).

1.5 Modelling frugivorous seed-dispersal

The influences of seed dispersal by animals on the spatial structure and dynamics of plant populations remains elusive (Cortes & Uriarte 2013). Most of the mechanistic models of seed dispersal, available in the literature, do only consider seed dispersal by wind (e.g., Levin and Muller-Landau 2000, Schurr et al. 2005, Nathan et al. 2002, 2011). However, recent work (Soons & Bullock 2008, Schleuning et al. 2011, Chama et al. 2013, Calvino-Cancela 2004, Caughlin et al. 2015, Mokotjomela et al. 2016) have mostly used simulations, statistical models and experimental approaches to study seed dispersal by frugivores. In fact, most of those available models neglect the spatial structure of plants population leading to possibly incorrect conclusions (Harada & Iwasa 1994).

1.6 Methodology

The methodology that we are going to use to build our frugivorous seed-dispersal model is called pair approximation method. It is a method of constructing a system of ordinary differential equation of a given population. We will consider the local abundance of plant population and its effects on the overall population growth. Pair approximation method captures the dynamics of both global and local densities of plants (Harada & Iwasa 1994). Thus, such a method will be efficient to study plant dynamics that are influenced by the local density of focal plants.

1.7 Aims and objectives

The interaction between fleshy-fruited plants and animals is mutualistic. Thus, there are benefits for both partners. The animals benefit is food from fruits pulp, leading to an increased density of animals equilibria, while plants benefits is seed dispersal leading to reduce level of plant clustering among other benefits.

Here, we propose a process-based mechanistic model of seed dispersal by frugivores. We consider both the global and the local densities of plants (Harada & Iwasa 1994), to explicitly model their effects on the plants growth and survivorship (Beckman & Rogers 2013, Caughlin et al. 2015). To make the model more realistic, we further consider three essential components of frugivorous seed dispersal, including the strength of the frugivore-plant mutualistic interaction, the efficiency of the seed disperser (Schupp 1993, Mokotjomela et al. 2016), as well as the germination probability of seeds (Chama et al. 2013, Calvino-Cancela 2004). For instance, the interaction strength among species is determined by species abundance and fruits availability (Schleuning et al.

2011). Specifically in our model, the interaction strength is characterized by the animals attack rate and the plants seed production rate. Finally, the model considers the animals benefit from the interaction with plants contributing to an increased animals density due to extra food resources. Using this model, we investigate how different factors, including seed production rate, plant local dispersal ability, frugivore dispersal efficiency and frugivore attack rate, alone or in combinations among them, can affect the spatial and temporal dynamics of plants.

Next, we are going to recall the pair approximation methodology that we use to build our frugivorous seed-dispersal model.

Chapter 2

Methods

Here, we briefly recall pair approximation method and introduce some bifurcation analysis that are needed for the main model in the next chapter.

2.1 Pair Approximation Method

Modelling spatially-explicit population dynamics often requires methodologies that consider the spatial patterns of a given population (Harada & Iwasa 1992, Hui et al. 2006). This can ensure more precise and accurate predictions of population densities and spatial distributions over time and space. Pair approximation considers population spatial structure and allows to construct a system of ordinary differential equations for both global and local densities of a given population. It is also called doublet decoupling approximation (Masuda 1994). It has been used in ecology (Harada & Iwasa 1992, Masuda 1994, Ellener 2001), epidemiology (Sato et al. 1994) and evolutionary biology (Harada 1999, Takenaka 1997). Pair approximation assumes that the growth of a single individual is influenced by its direct neighbors. Thus, the global density dynamics is consequently affected by the local density of the same population. Pair approximation neglects the effect of indirect neighbors (neighbor of the neighbor) of an individual. The simplicity of pair approximation allows to formulate spatially explicit dynamics in an analytic fashion (e.g. Hui & Li 2004, Hui & Richardson 2017). In contrast to pair approximation method, the mean-field approximation only considers the average density dynamics and neglects the effects of spatial structure and local density on the overall population growth. Neglecting the spatial structure of populations will lead to possibly incorrect predictions of population densities (Harada & Iwasa 1992). Instead, pair approximation provides more accurate predictions of populations dynamics than the mean-field approximation, and gives information on the spatial structure of populations. In particular, if the local density is greater than the global density, plants are clustered in space; equal local and global densities define the spatially random structure; otherwise plants are segregated in space

(Hui et al. 2006).

2.1.1 Plant-plant interaction model

Plant population growth is often influenced by biotic factors such as plant-plant and plant-animal interactions and abiotic factors such as plant-environment interaction. Here, we briefly present pair approximation model of plant-plant interaction (i.e., plants interact with their neighbors). We consider an infinitely large and regular lattice model for plant population dynamics (Harada & Iwasa 1994). Plants reproduce seeds to their nearest-neighboring sites in the lattice. We refer to those neighboring sites as local sites of focal plants. Each lattice site is either occupied (+ site) by an individual plant or empty (0 site). Seeds reproduced by a focal plant will fall down on its neighborhood and will only grow if they fall in empty local sites. All seeds falling in occupied sites will die. Thus, the final destination of a seed is an important determinant of its fate and overall plant population dynamics. Each site in the lattice will experience the following transitions:

1. Birth: $(+, 0) \xrightarrow{b} (+, +)$
2. Death: $+ \xrightarrow{d} 0$

where b and d are the natural death and birth rates of an individual plant. The pair $(., .)$ indicates the nearest-neighboring sites in the lattice. The nearest-neighboring site of an occupied site will eventually be occupied if a seed falls in it with a certain probability. We consider a homogeneous landscape and thus all seeds will experience the same environmental conditions. Indeed, the birth of new individual plants will depend on seed production rate and germination probability of produced seeds.



Figure 2.1: This diagram illustrates that a seed can only grow if it falls in an empty neighboring site or die if it falls in an already occupied site.

To begin with a simple model, we assume that seeds will germinate and survive if they fall in empty local sites in the neighborhood of a focal plant. However, falling in an empty site does not completely guarantee seed germination and seedling establishments. Later, we will develop a more precise lattice-model of seed dispersal and will discuss this in details. Now, let P_+ denote the probability that a randomly chosen lattice site is occupied by an individual plant, and P_0 denotes the probability that a randomly chosen lattice site is empty. Since the birth of a new offspring is restricted by the availability

of a vacant nearest-neighboring site, we consider $q_{0|+}$ to be the conditional probability that the nearest-neighboring site of a given occupied site is an empty site where a seed can settle and germinate. Let P_{0+} and P_{++} denote the probabilities of randomly chosen nearest-neighboring sites $(0, +)$ and $(+, +)$, respectively. The following equations are true by probability definitions:

$$\begin{aligned} P_{0+} &= P_{+0} \\ P_0 &= 1 - P_+ \\ q_{0|+} &= 1 - q_{+|+} \\ q_{0|+} &= \frac{P_{0+}}{P_+} \\ q_{+|+} &= \frac{P_{++}}{P_+} \end{aligned}$$

The probability densities P_+ and P_{++} are called the global densities of plants while $q_{+|+}$ is called the local density. Here, global density indicates the average density of plants everywhere in the lattice and local density refers to plant density in neighborhood of focal plants. The local density gives information about plant spatial distribution in the whole lattice (e.g., clustering). Since the birth of a new adult plant can only take place if the nearest-neighboring site of an occupied site is an empty site, then the plant global density dynamics is governed by the equation

$$\begin{aligned} \dot{P}_+ &= -dP_+ + bq_{0|+}P_+ \\ &= -dP_+ + b(1 - q_{+|+})P_+ , \end{aligned} \quad (2.1.1)$$

where the dot notation represents time derivative and the birth rate b is the probability that seeds will grow in the nearest-neighboring empty sites given that all seeds fall from the parent plant to the nearest-neighboring sites. Equation (2.1.1) can be written as

$$\dot{P}_+ = r_P P_+ \left(1 - \frac{q_{+|+}}{K_P}\right) , \quad (2.1.2)$$

where $r_P = b - d$, and $K_P = \frac{r_P}{b}$. We presume that r_P is a positive real number. In order to solve Equation (2.1.2), we must have an equation for the local density $q_{+|+}$. In doing so, we first differentiate both sides of the equation $q_{+|+} = \frac{P_{++}}{P_+}$ with respect to time in order to get

$$\dot{q}_{+|+} = -\frac{P_{++}}{P_+^2} \dot{P}_+ + \frac{1}{P_+} \dot{P}_{++} . \quad (2.1.3)$$

Second, following a similar way of obtaining Equation (2.1.1), we derive an equation for P_{++} which is given by:

$$\frac{dP_{++}}{dt} = -2dP_{++} + 2\frac{b}{z}P_{+0} + 2\frac{b}{z}(z-1)q_{+|0+}P_{+0} , \quad (2.1.4)$$

where z , defined the number of the nearest-neighboring sites of a focal plant, measures the local dispersal ability of plants to their neighborhoods. It is an essential element for limiting plant reproduction (Harada 1999). The first term indicates the transition of a $(+, +)$ pair to either $(+, 0)$ pair or $(0, +)$ pair, that is where the factor 2 comes from. In the second term, an occupied site contributes by a birth of an individual to its nearest-neighboring empty site with transition from $(+, 0)$ pair to $(+, +)$ pair or from $(0, +)$ pair to $(+, +)$ pair. The third term, the presence of an occupied site adjacent to the empty site of a given $(+, 0)$ pair may affect the transition of $(+, 0)$ to $(+, +)$, that is, the transition from $(+, 0, +)$ to $(+, +, +)$ or $(0 \rightarrow +)$ could be from any of the neighbors of the 0 site from the left or from the right. That is why we multiply by $q_{+|0+}$.

2.1.2 Ordinary pair approximation closure

There are several ways to approximate the probability density $q_{+|0+}$ (see Lucas 2012). One of them is called the ordinary pair approximation closure which assumes that the indirect effect of the neighbor-of-the neighbor is small and thus neglects it. In other words, it assumes that $q_{+|0+} \approx q_{+|0}$. Since we have $P_{+0} = P_{0+} = P_+ q_{0|+} = P_+(1 - q_{+|+})$, then

$$q_{+|0+} \approx q_{+|0} = \frac{P_{+0}}{P_0} = \frac{P_{0+}}{1 - P_+} = \frac{(1 - q_{+|+})P_+}{1 - P_+}. \quad (2.1.5)$$

By substituting Equation (2.1.5) into Equation (2.1.4) and substituting the result into Equation (2.1.3) and rearranging we get:

$$\begin{aligned} \dot{q}_{+|+} = & -q_{+|+} [d + b(1 - q_{+|+})] \\ & + \left[\frac{2b}{z} \left(1 + (z - 1) \frac{(1 - q_{+|+})P_+}{1 - P_+} \right) \right] (1 - q_{+|+}). \end{aligned} \quad (2.1.6)$$

Equation (2.1.6) describes the plant local density dynamics. Now we have a dynamical system of two ordinary differential equations governing the plant global and local dynamics in the whole lattice and is given by

$$\begin{aligned} \dot{P}_+ = & -dP_+ + b(1 - q_{+|+})P_+ \\ \dot{q}_{+|+} = & -q_{+|+} [d + b(1 - q_{+|+})] \\ & + \left[\frac{2b}{z} \left(1 + (z - 1) \frac{(1 - q_{+|+})P_+}{1 - P_+} \right) \right] (1 - q_{+|+}). \end{aligned}$$

Equations (2.1.1) and (2.1.6) implicitly describe the plant-plant interaction (interaction within neighboring sites) and consider the effect of local density on the overall plant population growth. Pair approximation method correctly predict changes in plant densities and plant spatial structure (Harada & Iwasa 1992).

2.1.2.1 Mathematical Analysis

The steady states of the plant-plant interaction model can be obtained analytically by solving the two equations $\dot{P}_+ = 0$ and $\dot{q}_{++} = 0$ for P_+ and q_{++} . We get the following mathematical equilibriums

$$P_+^* = \frac{d(z-1)}{d-b(z-1)} + 1, \quad q_{++}^* = 1 - \frac{d}{b} \quad (2.1.7)$$

$$P_+^* = 0, \quad q_{++}^* = \frac{z+2}{2z} \pm \frac{\sqrt{(b+d)^2 z^2 - 4b^2 z + 4bdz + 4b^2} \pm dz}{2bz}. \quad (2.1.8)$$

In Equation (2.1.8), the trivial equilibrium $P_+ = 0$ corresponds to the absence or extinction of plants. Pair approximation defines q_{++} to be the conditional probability that the nearest neighbor of a given occupied site is occupied. Therefore, this definition assumes that $P_+ \neq 0$. However, if there is no plants at all in the whole lattice ($P_+ = 0$) then q_{++} must equal to zero as well. The positive equilibrium P_+^* in Equation (2.1.7) becomes zero (i.e., plants must go extinct) when $b = dz/(z-1)$. The positive equilibrium P_+^* is globally stable and the trivial equilibrium (extinction equilibrium) is unstable.

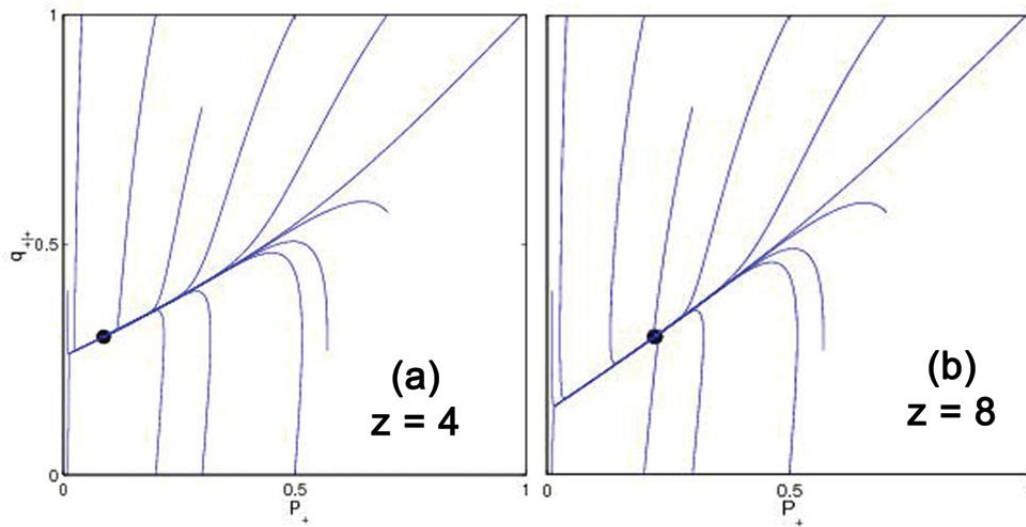


Figure 2.2: Trajectories of plant dynamics for two different number of neighboring sites from left to right ($z = 4$ and $z = 8$). The filled circle represent stable equilibrium of the system. Parameters used are: $b = 0.1$ and $d = 0.07$.

Trajectories in Figure 2.2 show the global stability of positive equilibria for both global and local densities of plants when they exist. In this model, plant population will only persist when the birth rate b is greater than the death rate d . Plant natural dispersal ability is limited by the number of nearest-neighboring sites z . Higher number of z facilitates seed dispersal in the neighborhoods of focal plants. Also this will result in an increase in plant global

density and a decrease in plant intraspecific competition for resources (Figure 2.2).

2.1.3 Extended pair approximation

Another possible closure to approximate the probability density $q_{+|0+}$ is called the extended pair approximation closure (Lucas 2012). It assumes that

$$q_{+|0+} = \frac{P_+ + 2q_{+|+} - 3P_+q_{+|+}}{3(1 - P_+)} . \quad (2.1.9)$$

By substituting Equation (2.1.9) into Equation (2.1.4) and substituting the result into Equation (2.1.3) and rearranging we get:

$$\begin{aligned} \dot{q}_{+|+} = & -\frac{1}{P_+} (P_+ + b(1 - q_{+|+})) q_{+|+} - 2P_+q_{+|+} - \frac{2b}{z} (1 - q_{+|+}) \\ & + \frac{2b(z-1)P_+ (1 - q_{+|+}) (P_+ + 2q_{+|+} - 3P_+q_{+|+})}{3z(1 - P_+)} . \end{aligned} \quad (2.1.10)$$

Equations (2.1.1) and (2.1.10) are now the new dynamical systems that describes changes in the global and local densities of plant population.

2.1.4 Mean-field approximation

A simple way to predict populations dynamics is to neglect its spatial structure. Mean-field approximation predicts the average density of a given population, neglects the spatial patterns in population dynamics and the spatial correlation between lattice sites (Harada 1999). Thus, it incorrectly predicts population densities. It assumes that the local density is the same as the global density (*i.e.*, $q_{+|+} = P_+$). Hence, plants are randomly distributed in space, and grow according to the following logistic equation

$$\dot{P}_+ = r_P P_+ \left(1 - \frac{P_+}{K_P}\right) . \quad (2.1.11)$$

obviously, plant population dynamics is influenced by the neighboring sites in the lattice which we can not neglect. We conclude that pair approximation method predicts plant densities more precisely and accurately than the mean-field approximation.

2.2 Bifurcation analysis

Differential equations that describe the behavior of natural systems often contains one or more parameters. In practice, those parameters are usually approximations of exact values and therefore system solutions are also approximations of reality. Natural phenomenons are often complex and a dynamical

system that governs such a phenomenon is thus nonlinear. The qualitative behavior of a given system may change when we vary a single or more parameters. This change is known as bifurcation and it usually occurs in complex and nonlinear systems. The parameter that is varied is called bifurcation parameter. More details on bifurcation theory can be found in Kuznetsov (2013) and Iooss & Joseph (2012).

However, the purpose of this thesis is not to present bifurcation theory. We rather briefly recall two simple types of bifurcations which would help the reader with no prior knowledge of bifurcation theory to understand the analysis of our main model. First, consider the following one-dimensional dynamical system

$$\dot{x} = f(x) . \quad (2.2.1)$$

The equilibrium points of Equation (2.2.1) (also called fixed or stationary points or steady states) are the solutions of $f(x) = 0$. Assume that the solution of $f(x) = 0$ is given by $x = x^*$, where x^* is called equilibrium point. The value of $f'(x^*)$, where the "'' notation represents f derivative, is known as the eigenvalue of the system which gives information about the stability of the system. The fixed point x^* is said to be stable if $f'(x^*) < 0$ and unstable if $f'(x^*) > 0$. The first derivative fails to determine the stability of x^* when $f'(x^*) = 0$. If a dynamical system has two fixed points, then they are stable if their corresponding eigenvalues are both negative and unstable if at least one of them is positive. If the eigenvalues have the same sign, the fixed point is called a node or a focus and it is called a saddle if the eigenvalues have different signs. Next, we briefly review two types of bifurcation for the sake of this thesis.

2.2.1 Saddle-node bifurcation

In this type of bifurcation, fixed points of a dynamical system can be created and destroyed when a parameter is varied. The normal form of saddle-node bifurcation is given the following example

$$\dot{x} = r + x^2, \quad (2.2.2)$$

where r is the bifurcation parameter of the system that we vary. First, we find the fixed points of Equation (2.2.2) which are given by $x_1^* = \sqrt{-r}$ and $x_2^* = -\sqrt{-r}$. The stability of these fixed points depend on the value of r . There are three possible values for the parameter r : $r < 0$, $r = 0$ and $r > 0$ which give three different qualitative structure of the system. For $r < 0$, there are two fixed points, x_1^* is stable (i.e., $f'(x_1^*) < 0$) and x_2^* is unstable (i.e., $f'(x_2^*) > 0$). For $r = 0$, there is only one fixed point $x^* = 0$ and the first derivative fails to determine its stability. For $r > 0$, there is no fixed point at all. Changes in the qualitative behavior of the system are shown in Figure 2.3.

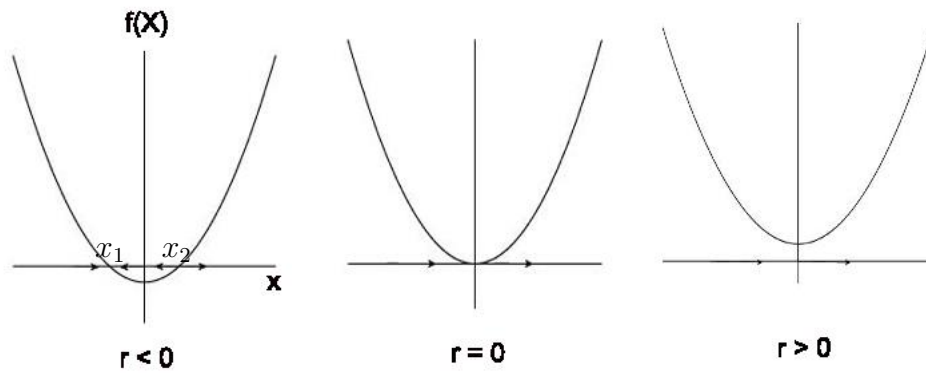


Figure 2.3: Saddle-node bifurcation: qualitative changes in the system when the bifurcation parameter r is varied.

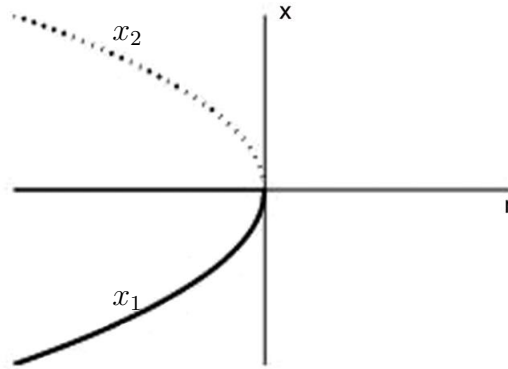


Figure 2.4: Saddle-node bifurcation diagram. The solid curve is the stable branch and the dashed curve is unstable branch.

2.2.2 Transcritical bifurcation

The fixed points of a given dynamical system cross and may exchange their stability when a parameter is varied. This is referred to as transcritical bifurcation where fixed points are never destroyed. There is always a stable and unstable fixed point. Those fixed points interchange their stability when they collide. The stable one would become unstable and vice versa. The normal form of this type of bifurcation is given by the following example

$$\dot{x} = rx - x^2, \quad (2.2.3)$$

where r is the bifurcation parameter of the system that we vary. There are two fixed points of Equation (2.2.3) which are: $x_1^* = 0$ and $x_2^* = r$. For $x_1^* = 0$,

we have $f'(0) = r$ and thus it is only stable when r is negative. For $x_2^* = r$, we have $f'(r) = -r$ and thus it is only stable when r is positive. Changes in the qualitative behavior of the system are shown in Fig

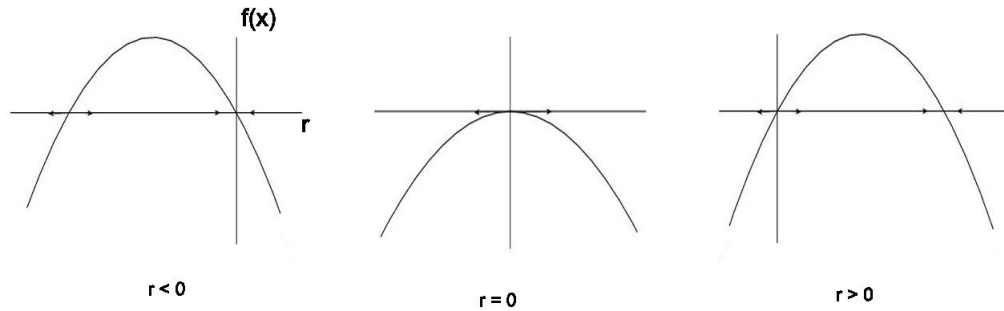


Figure 2.5: Transcritical bifurcation: qualitative changes in the system when the bifurcation parameter r is varied

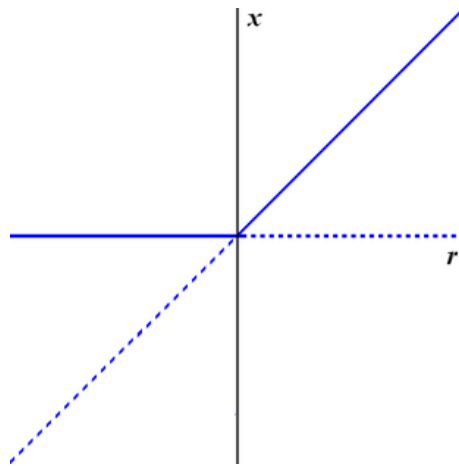


Figure 2.6: Transcritical bifurcation diagram. The solid curve is the stable branch and the dashed curve is unstable branch. The intersection point is where the two branches meet and exchange their stability

These two types of bifurcations are useful for the numerical analysis of our frugivorous seed-dispersal model. However, there are other types of bifurcations that are not needed here for the sake of this thesis.

Chapter 3

Model

3.1 Plant-frugivore interaction model

We now use pair approximation method to model the plant-frugivore mutualistic interaction and seed dispersal. Plants provide frugivorous animals with extra food resources while frugivores disperse seeds away from the parent plants, decreasing local intraspecific competition and plant clustering. Successful frugivore-mediated seed dispersal can contribute to the plant long-term fitness and preserve plants population from extinction. To model plant-frugivore mutualistic interaction, we first divide the seeds produced by focal plants into two groups; eaten and non-eaten seeds. The non-eaten seeds will grow locally, in the neighborhoods of their parent trees, if they fall in empty local sites while the eaten seeds will be dispersed by frugivores globally in a homogeneous landscape. We then consider the frugivore dispersal cost and assume that the eaten seeds will experience some risk during dispersal, and only a fraction of them will be dispersed globally in the lattice and can only germinate if they fall in empty sites. Furthermore, we consider the strength of plant-frugivore interaction which is characterized by the frugivore attack rate in the model. However, the interaction strength between plants and frugivores is also influenced by fruits and frugivore species abundances. We further consider the germination probability of the dispersed seeds either locally by their parental plants or globally by frugivorous animals.

Plants produce seeds at rate m (seed production rate) and frugivorous animals consume the encountered seeds with probability a (frugivore attack probability). We assume that animal have a random spatial distribution and forage randomly over space, therefore the number of seeds eaten by animals in a time interval follows a Poisson distribution with mean $\lambda = aAmP_+$ which is the expected number of eaten seeds per unit time. The fraction of seeds that are not eaten in the unit time is thus given by $e^{-\lambda}$, while the fraction of seeds that are eaten is $(1 - e^{-\lambda})$. The proportion of non-eaten seeds will grow locally in the

neighborhoods of focal plants if they fall in empty sites. The eaten seeds pass through the digestive system of frugivores and experience some risk, so the proportion of seeds that are being dispersed and that can grow globally if they find empty global sites is $\mu(1 - e^{-\lambda})$. The fraction μ is the dispersal efficiency of frugivores which measures the proportion of seeds that will be successfully dispersed in safe sites for germination and establishment, while $(1 - \mu)$ measures the dispersal cost or the proportion of seeds that have been lost during seed transportation. Of course, not all seeds that have been dispersed either locally in the neighborhood of plants or globally by animals will germinate, but only a fraction of them will germinate with a germination probability g . We therefore consider seed germination probability in the model. For simplicity, we presume that the lattice is regular and homogeneous and all dispersed seeds in the landscape will experience the same environmental conditions.

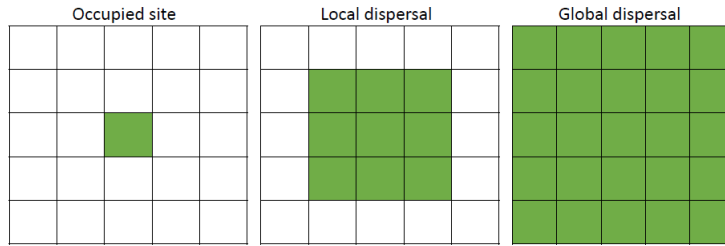


Figure 3.1: This figure illustrates the local and global dispersal in a homogeneous and regular lattice. Single occupied site (left), local dispersal to the neighborhood (middle), global dispersal in the whole lattice (right)

The rate of change of the global density of plants is given by

$$\dot{P}_+ = -dP_+ + ge^{-aAmP_+}(1 - q_{+|+})mP_+ + g\mu(1 - e^{-aAmP_+})mP_+(1 - P_+), \quad (3.1.1)$$

where d is the natural death rate of plants, and that $gm = b$ is the intrinsic birth rate of new adult plants. The second term in equation (3.1.1) refers to the local birth of the non-eaten seeds in the neighborhood of parent trees, while the third term refers to the global birth of new plants due to seed dispersal by frugivores. In our model, frugivorous animals are assumed to have another food resources and they can survive without the plants we consider. Therefore, in the absence of plants, frugivores can grow according to the logistic equation. Given plant-frugivores mutualistic interaction, the eaten seeds will be converted into the biomass of frugivore with conversion rate α . Thus the governing equation of frugivore dynamics after interaction is given by

$$\dot{A} = r_AA \left(1 - \frac{A}{K_A}\right) + \alpha(1 - e^{-aAmP_+})mP_+, \quad (3.1.2)$$

where r_A and K_A are the intrinsic growth rate and carrying capacity of frugivores, respectively. The last term in equation (3.1.2) indicates the plants con-

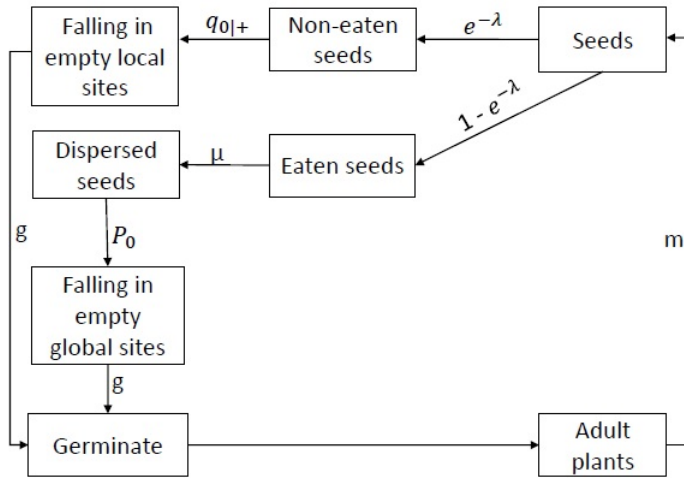


Figure 3.2: This flow chart illustrates and summaries the modelling process. Animals interact with plants and eat their seeds with certain probability. The probability that none of the seeds is eaten is given by $e^{-\lambda}$, while the probability that animals eat the seeds is given by $(1 - e^{-\lambda})$. The non-eaten seeds will germinate with probability g if they fall in empty local sites with probability $q_{0|+}$. The eaten seeds pass through the digestive system of animals where seeds will experience some risk, measured by $(1 - \mu)$, before being dispersed globally. The fraction of the seeds that will be dispersed can only germinate with probability g if they fall in empty global sites with probability P_0 . The new adult plants will produce seeds at rate m .

tribution to the animals biomass. In order to obtain the full system that governs the plant-frugivore mutualistic interaction, equations (3.1.1) and (3.1.2) must be completed by an equation for the local density $q_{+|+}$.

Here we derive an equation for the local density $q_{+|+}$. Given $q_{+|+} = \frac{P_{++}}{P_+}$, then

$$\dot{q}_{+|+} = -\frac{P_{++}}{P_+^2}\dot{P}_+ + \frac{1}{P_+}\dot{P}_{++}, \quad (3.1.3)$$

where P_{++} is the probability that a randomly chosen two neighboring sites are both occupied. We already have \dot{P}_+ then we must find an equation for the global density P_{++} (see, Harada & Iwasa 1994), which is given by

$$\begin{aligned} \dot{P}_{++} = & -2dP_{++} + 2\frac{gm}{z}e^{-aAmP_+}P_{+0} + 2\frac{gm}{z}(z-1)e^{-aAmP_+}q_{+|0+}P_{+0} \\ & + 2gm\mu(1 - e^{-aAmP_+})P_+P_{+0} \end{aligned} \quad (3.1.4)$$

Where z is the number of the nearest-neighboring sites. The first term indicates the transition of a $(+, +)$ pair to $(+, 0)$ pair or $(0, +)$ pair, that is where the

factor 2 comes from. In the second and third terms, we refer to the birth of the non-dispersed seeds. In the second term, an occupied site contributes by a birth of an individual to its nearest-neighboring empty site with transition from $(+, 0)$ pair to $(+, +)$ pair or from $(0, +)$ pair to $(+, +)$ pair. The third term, the presence of an occupied site adjacent to the empty site of a given nearest-neighboring sites $(+, 0)$ may affect the transition of $(+, 0)$ to $(+, +)$, that is, the transition from $(+, 0, +)$ to $(+, +, +)$ or $(0 \rightarrow +)$ could be from any of the neighbors of the 0 site. That is why we multiply by $q_{+|0+}$. The pair approximation method neglects the effect of the neighbor-of-the neighbor, therefore $q_{+|0+} \approx q_{+|0}$. We have

$$P_{+0} = P_{0+} = P_+ q_{0|+} = P_+ (1 - q_{+|+})$$

$$q_{+|0+} \approx q_{+|0} = \frac{P_{+0}}{P_0} = \frac{P_{0+}}{1 - P_+} = \frac{(1 - q_{+|+})P_+}{1 - P_+}$$

The P_{++} dynamics equation can be rewritten as

$$\begin{aligned} \dot{P}_{++} = & -2dP_{++} + 2\frac{gm}{z}e^{-aAmP_+}P_+(1 - q_{+|+}) \\ & + 2\frac{gm}{z}(z - 1)e^{-aAmP_+}\frac{(1 - q_{+|+})P_+}{1 - P_+}P_+(1 - q_{+|+}) \\ & + 2\mu gm(1 - e^{-aAmP_+})P_+P_+(1 - q_{+|+}) . \end{aligned} \quad (3.1.5)$$

Equation (3.1.5) can be simplified to

$$\begin{aligned} \dot{P}_{++} = & -2dP_{++} + 2\frac{gm}{z}e^{-aAmP_+}P_+(1 - q_{+|+}) \\ & + 2\frac{gm}{z}(z - 1)e^{-aAmP_+}\frac{(1 - q_{+|+})^2P_+^2}{1 - P_+} \\ & + 2g\mu(1 - e^{-aAmP_+})mP_+^2(1 - q_{+|+}) . \end{aligned} \quad (3.1.6)$$

In order to have a system that describes the dynamics of the global density P_+ , local density $q_{+|+}$ and animals density A , we must obtain an equation for the local density $q_{+|+}$. We already have equations for the global densities P_+ and P_{++} , then will use the following equation to get an equation describing the local density dynamics.

$$\dot{q}_{+|+} = -\frac{P_{++}}{P_+^2}\dot{P}_+ + \frac{1}{P_+}\dot{P}_{++} \quad (3.1.7)$$

$$-\frac{P_{++}}{P_+^2}\dot{P}_+ = dq_{++} - gme^{-aAmP_+}q_{++}(1 - q_{++}) - g\mu m(1 - e^{-aAmP_+})q_{++}(1 - P_+) \quad (3.1.8)$$

$$\begin{aligned} \frac{1}{P_+}\dot{P}_{++} = & -2dq_{++} + \frac{2gm}{z}e^{-aAmP_+}(1 - q_{++}) \\ & + \frac{2gm}{z}(z - 1)e^{-aAmP_+}\frac{(1 - q_{++})^2P_+}{1 - P_+} \\ & + g\mu(1 - e^{-aAmP_+})mP_+(1 - q_{++}) . \end{aligned} \quad (3.1.9)$$

Adding equations (3.1.8) and (3.1.9) together we get

$$\begin{aligned} \dot{q}_{++} = & -dq_{++} + gme^{-aAmP_+}(1 - q_{++})\left(\frac{2}{z} - q_{++}\right) \\ & + g\mu(1 - e^{-aAmP_+})m(2P_+ - P_+q_{++} - q_{++}) \\ & + \frac{2gm}{z}(z - 1)e^{-aAmP_+}\frac{(1 - q_{++})^2P_+}{1 - P_+} . \end{aligned} \quad (3.1.10)$$

Now we have a system of three nonlinear ordinary differential equations governing the ecological dynamics of the plant-frugivore mutualistic interaction. Next, we are going to analyze our model numerically and to investigate the behavior of the system without and with animal-mediated seed dispersal. The full dynamical system is given by the following nonlinear differential equations

$$\begin{aligned} \dot{P}_+ = & -dP_+ + ge^{-aAmP_+}(1 - q_{++})mP_+ + g\mu(1 - e^{-aAmP_+})mP_+(1 - P_+) \\ \dot{A} = & r_A A \left(1 - \frac{A}{K_A}\right) + \alpha(1 - e^{-aAmP_+})mP_+ \\ \dot{q}_{++} = & -dq_{++} + gme^{-aAmP_+}(1 - q_{++})\left(\frac{2}{z} - q_{++}\right) \\ & + g\mu(1 - e^{-aAmP_+})m(2P_+ - P_+q_{++} - q_{++}) \\ & + \frac{2gm}{z}(z - 1)e^{-aAmP_+}\frac{(1 - q_{++})^2P_+}{1 - P_+} \end{aligned}$$

The initial conditions of this model for both plant and animal densities are prescribed (see Results Section or Matlab codes in Appendix).

Next, we will analyze this model numerically and compare the plant global and local density dynamics without and with animals for different seed production rates. We then focus on plant density equilibria and we study the effect of habitat quality (quantified by the seed production rate m) and natural intrinsic plant dispersal (quantified by the number of neighboring sites z) on the

two ecological scenarios of plant population. Furthermore, we focus on the plant-animal interaction and we study the effects of the animals attack rate a and dispersal efficiency μ on plant density equilibria, and we conclude with investigating the effects of all combinations of parameter pairs on plant dynamics. We have used Matlab continuation package (MATCONT) to analyze our model (Dhooge et al. 2003).

Table 3.3 shows the summary of the variables and parameters we use in our frugivorous seed-dispersal model, with their definitions.

Variable	Definition	Unit
P_+	Global density of plants	Dimensionless
q_{++}	Local density of plants	Dimensionless
A	Animals density	# of Animals per unit area
Parameter	Definition	Unit
b	Birth rate of plants	$\frac{1}{\text{time}}$
d	Natural death rate of plants	$\frac{1}{\text{time}}$
m	Seed production rate per unit density of plants	$\frac{\# \text{ of seeds}}{\text{time}}$
g	Germination probability per seed	$\frac{1}{\# \text{ of seeds}}$
r_A	Intrinsic growth rate of animals	$\frac{1}{\text{time}}$
K_A	Carrying capacity of animals	# of animals per unit area
z	Number of nearest-neighboring sites	Dimensionless
a	Animals per-capita attack probability	$\frac{1}{\# \text{ of animals per unit area}}$
μ	Dispersal efficiency	Dimensionless
α	Conversion rate	$\frac{\# \text{ of animals per unit area}}{\# \text{ of seeds}}$

Figure 3.3: Variables and parameters of frugivorous seed-dispersal model

Chapter 4

Main Results

We here present the main results from frugivorous seed-dispersal model. Both the dynamics of plant global and local densities and the density of frugivores are presented.

4.1 Plants dynamics

Here, we show the different ecological scenarios for plant population without and with frugivore-mediated seed dispersal, under different environmental and demographic conditions. We further show how plant global and local densities are affected by habitat quality (increasing seed production rate in our model) and intrinsic local dispersal ability of plants (quantified by the number of neighboring sites z). After this, we then study the effect of frugivore attack rate and dispersal efficiency on plant densities. Finally, we assess the combined effects of pairs of environmental, demographic, and animal dispersal parameters.

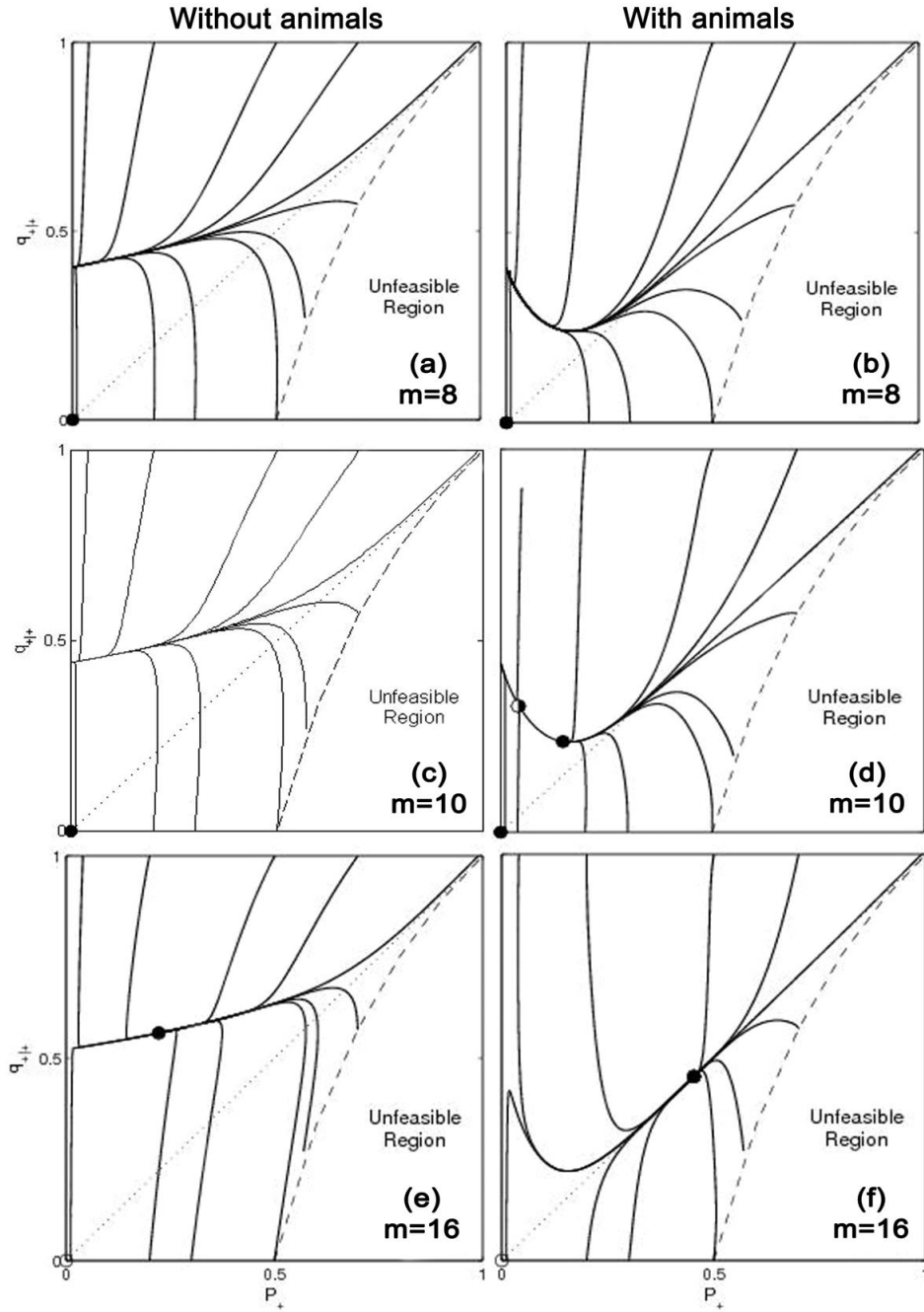


Figure 4.1: Plant global and local dynamics without and with animals. Three different levels seed production rates from top to bottom ($m = 8, m = 10$ and $m = 16$), representing a gradient of increasing habitat quality. The first column represents the plant dynamics with no animals while the second column presents the plant dynamics with animals. The dotted line on the diagonal corresponds to the mean-field approximation where the global and local densities of plants are equal and plants are randomly distributed along this line, aggregated (clustered) above the diagonal and segregated below the diagonal. Filled circles correspond to stable equilibria, open circles correspond to unstable equilibria and the half-filled circle corresponds to saddle point. The regions below the dashed line are unfeasible regions. The parameters used are: $d = 0.07$, $a = 0.1$, $r = 1$, $k = 10$, $\alpha = 2$, $z = 2$, $g = 0.01$ and $\mu = 0.8$.

Trajectories in Figure 4.1a and b show that plants can not persist if the seed production rate is low, no matter if they interact with animals or not (extinction scenarios). However, when the seed production rate is higher ($m = 10$ in Figure 4.1c and d), efficient frugivores can prevent plants from extinction, changing the ecological scenario from extinction to conditional persistence, in which, together with the stable extinction equilibrium, a second alternative stable state of plant persistence is present. The basins of attraction of the two alternative attractors are separated by the stable manifold of the saddle (half-filled dot in Figure 4.1d), and the attained regime depends on the initial conditions of the system. For higher seed production rate ($m = 16$, Figure 4.1e and f), frugivorous animals increase the global density and decrease the local density of plants, making plant randomly distributed in space (equilibrium on the diagonal), see Figure 4.1e and f. Therefore, fruit-eating animals can change the spatial structure of plant species and determine their abundances. In fact, this also indicates that animals reduce the plants intraspecific competition for resources by dispersing seeds from more clustered areas to global empty sites (Figure 4.1e and f).

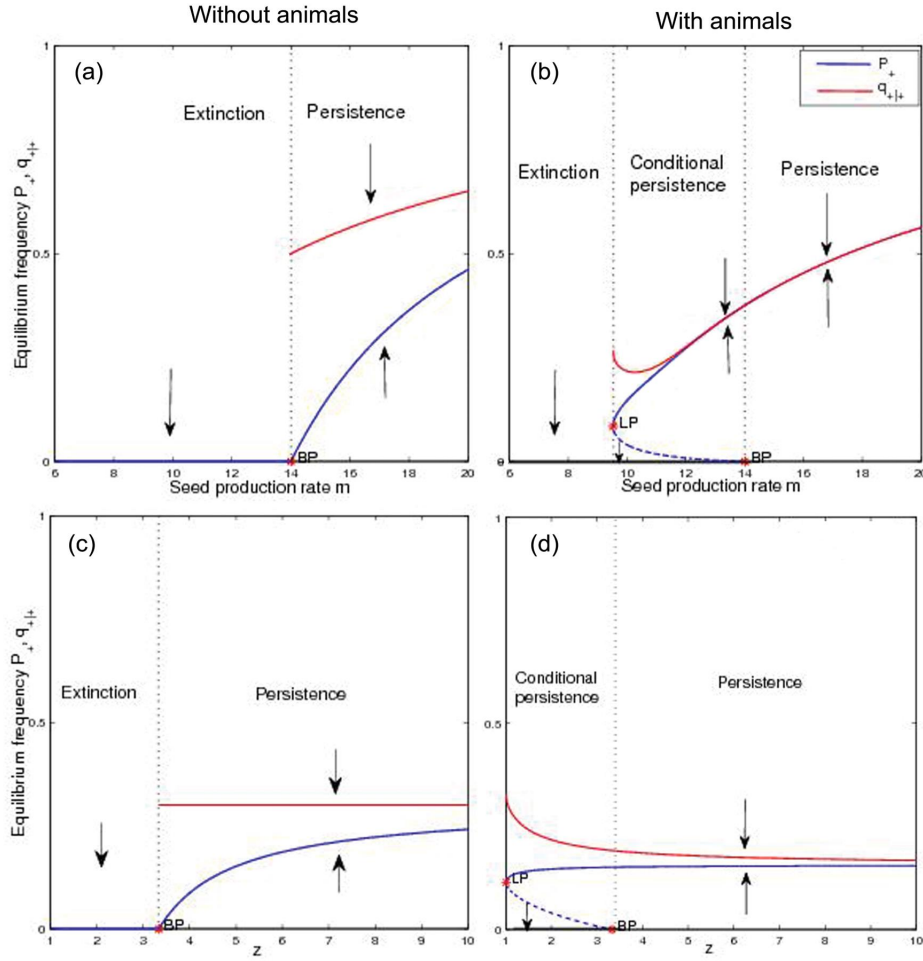


Figure 4.2: Changes in equilibrium of the global and local densities of plants when the seed production rate (first row) and the number of the nearest-neighbor sites (second row) vary. The first column and the second column represent the equilibrium changes without and with animals, respectively. The dotted lines separate these regions and the solid lines (blue and red) are the equilibrium curves. The dashed line (blue) of the equilibrium density P_+ refers to the unstable equilibrium and the solid line (blue) refers to the stable equilibrium of P_+ . The labels LP and BP indicate the limit-point (saddle-node) and branch-point (transcritical) bifurcations, respectively. In each panel, there are either two or three plant ecological scenarios: extinction, conditional persistence and persistence. Conditional persistence means either extinction or persistence, depending on the initial condition of plants density. All other parameters at their reference values: see caption of Figure 4.1 and $m = 10$.

Habitat quality variation can affect the ecological dynamics and the spatial distribution of plants as shown in Figure 4.1. Low seed production rate may drive plants to extinction even if animals disperse the seeds of plants. In Figure 4.2a, without animal-mediated seed dispersal, we have two regions which are stable extinction and stable persistence, describing the two scenarios of Figure 4.1a, c and e. There, plants can only persist if the seed production rate crosses the threshold of the branch-point (transcritical) bifurcation, at which the extinction equilibrium and the persistence equilibrium branches intersect and exchange their stability. But with animals dispersing the seeds, plants have a chance to persist even before that threshold, specifically between the limit-point (saddle-node) and the branch-point (transcritical) bifurcations. Therefore animal dispersal allows (conditional) plant persistence for lower habitat quality, provided the initial conditions of plant densities are sufficient to converge to the persistence equilibrium. At $m = 10$ till approximately $m = 12$ in Figure 4.2b, the equilibrium of the local density of plants is higher than the equilibrium of the global density which means plants are more clustered in space. Thereafter, both equilibriums are equal and animals change the plant distribution from cluster to random.

For the number of the nearest-neighboring sites z , without animals plants go extinct when z is less than 4 (Figure 4.2c), but with animal-mediated seed dispersal, plants can persist even if z is less than 4 (Figure 4.2d). If the number of the nearest-neighboring sites is relatively high, plants are more likely to have more local neighbors that can affect their growth and there is a higher chance of natural dispersal to the empty nearest-neighboring sites which will eventually be occupied. That is why, in Figure 4.2d, the equilibrium of $q_{+|+}$ is higher than the equilibrium of P_+ for higher values of z .

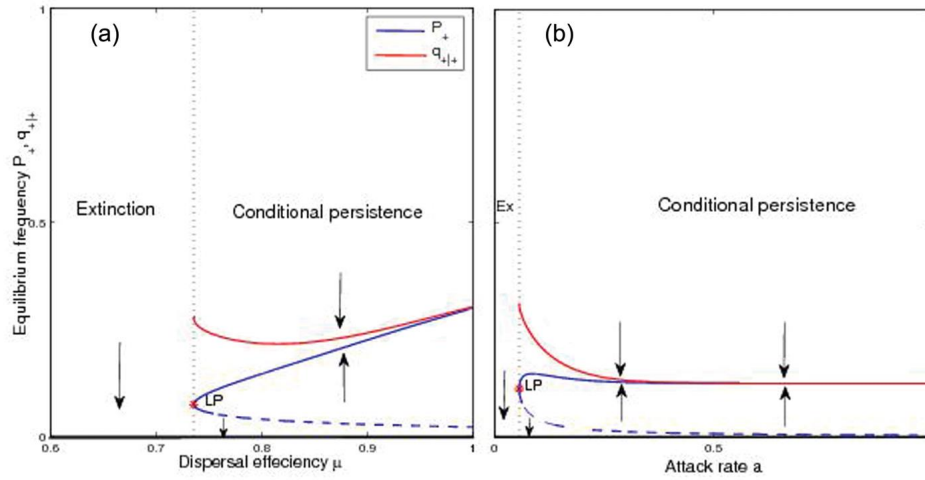


Figure 4.3: Changes in equilibrium of the global and local densities of plants when the dispersal efficiency (first column) and the attack rate (second column) vary. The dotted lines separate these regions and the solid lines (blue and red) are the equilibrium curves for the global and local densities of plants. The dashed line (blue) of the equilibrium density P_+ refers to the unstable equilibrium and the solid line (blue) refers to the stable equilibrium of P_+ . The label LP indicates the limit-point bifurcation. In each panel, there are two plant ecological scenarios which are extinction and conditional persistence. All parameters at their reference values.

Dispersal efficiency of frugivores μ , (Figure 4.3a) can preserve plant species and prevent them from extinction while inefficient seed dispersers can catastrophically drive plants to extinction when the dispersal efficiency is decreased below the threshold characterized by the limit-point (LP) bifurcation. Therefore, the LP separates the extinction and conditional persistence regions. Plants can also go extinct if the interaction strength is low or if only a few seeds are eaten. In other words, if the animals attack rate a is low (see Figure 4.3b). In both Figure 4.3a and b, the equilibrium of q_{++} is higher at the beginning but when we increase μ and a the equilibrium of P_+ and q_{++} have the same value and plant are distributed randomly.

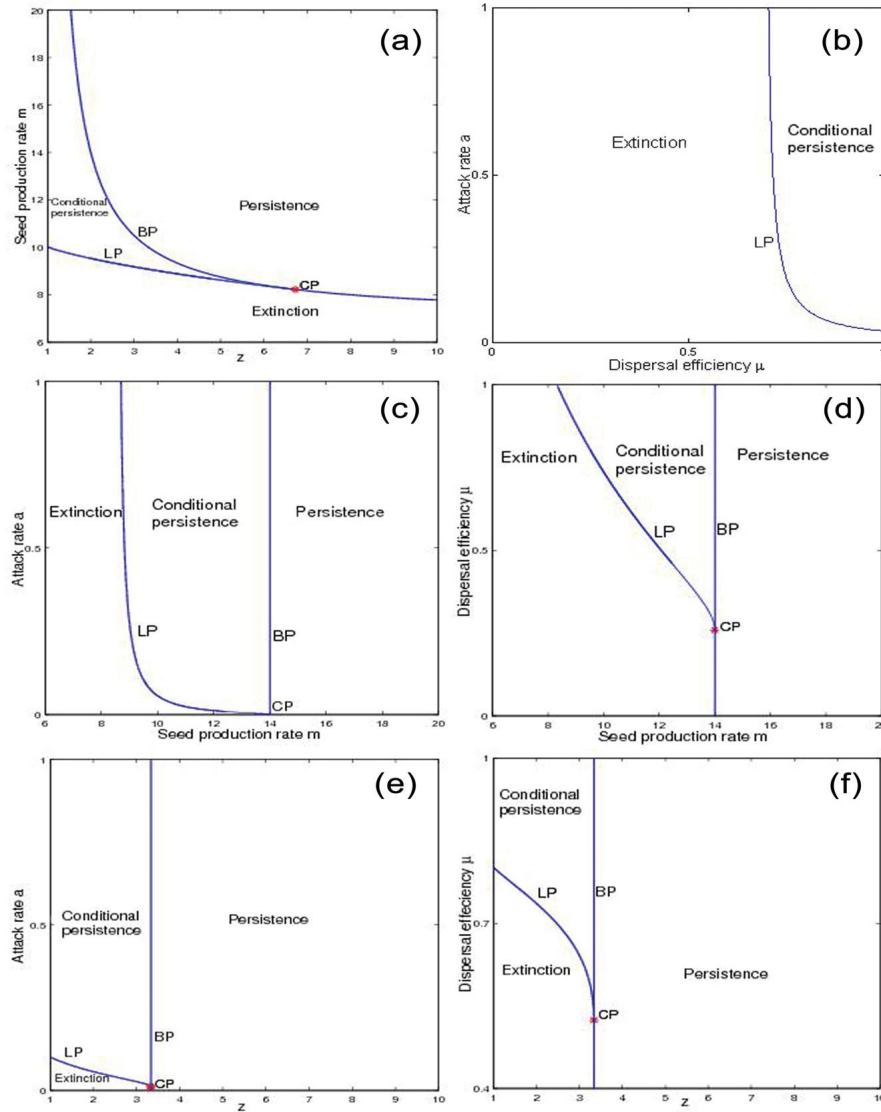


Figure 4.4: Changes in plant ecological scenarios with pairs of parameters. Lines represent limit-point and branch-point bifurcation curves. In each panel, there are either two or three parameter regions which are extinction, conditional persistence and persistence of plants. The labels LP, BP and CP indicate the limit-point, the branch-point and the cusp-point bifurcations, respectively. The cusp point is where limit- and branch-point bifurcation curves meet. All other parameters at their reference values.

Figure 4.4 shows the effect of parameter pairs on the three different ecological scenarios, i.e., extinction, conditional persistence, and persistence. In Figure 4.4a, plants conditionally persist if values of the seed production rate m and

the number of neighboring sites z lie between the limit- and branch-point bifurcation curves, and plants unconditionally persist if the values of m and z lie above the branch-point bifurcation curve. Moreover, Figure 4.4a also shows that if the habitat quality is low (characterized by lower values of m), plants will go extinct even if the number of neighboring sites z is high. Indeed, the efficiency of fruit-eating animals is crucial to preserve plant species. However, animals efficiency does not prevent plants from extinction if the attack rate a is very low (Figure 4.4b). The limit-point bifurcation curve in (Figure 4.4b) can be crossed horizontally (from left to right) and plant dynamics can shift from the extinction region to the persistence region provided that μ crosses the limit-point bifurcation (from left to right) in Figure 4.3a and a crosses the limit-point bifurcation (from left to right) in Figure 4.3b. However, Figure 4.4e shows that nonaggressive animals do also drive plants to extinction if the number of the neighboring sites z is less than 4. Figure 4.4e and f show that for any chosen values of μ and a between 0 and 1, plants can still persist as long as the number of neighboring sites z is higher than 3. Increases in the number of the neighboring sites z would help plants to persist even if the dispersal risk is high, but if z is less than 4 plants can only conditionally persist even if animals are very efficient (Figure 4.4f). Furthermore, Figure 4.4c and d show that plants unconditionally persist if the branch-point bifurcation curves have been crossed horizontally (from left to right) in both panels. Plants conditionally persist if the values of the seed production rate m and the attack rate a lie between the limit- and branch point bifurcation curves (Figure 4.4c). However, and if the values of the seed production rate m and the dispersal efficiency μ lie between the limit- and branch-point bifurcation curves (Figure 4.4d) plants go extinct.

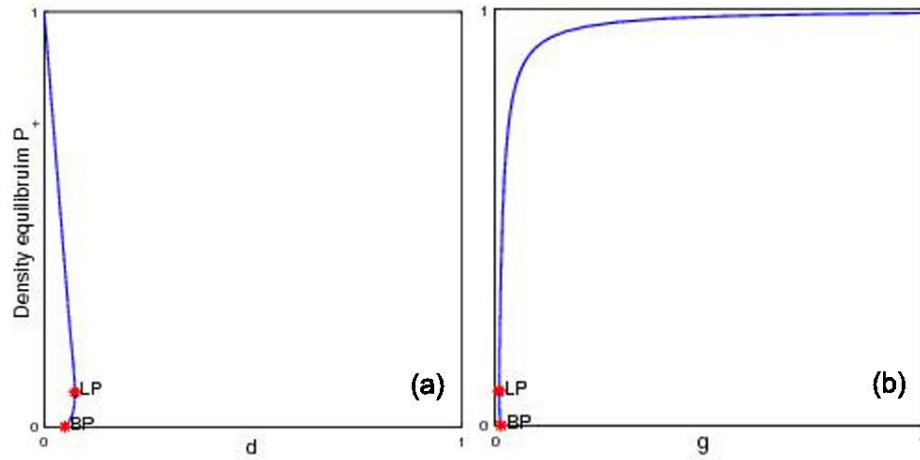


Figure 4.5: Changes in equilibrium of the global density of plants when the death rate (first column) and seed germination probability (second column) vary. The labels LP and BP indicate the limit-point and the branch-point bifurcation, respectively. In each panel, there are two plant ecological scenarios which are extinction and conditional persistence. All parameters at their reference values.

High natural death rate of plants leads to extinction of plant density equilibria even if seeds are dispersed either naturally or by frugivorous animals (Figure 4.5 a). An increase in seed germination probability allow plant global and local persistence provided that plant fecundity is high enough (Figure 4.5 b).

4.2 Frugivores dynamics

We have shown the plants benefit from frugivorous seed-dispersal. As a result of plant-frugivore mutualistic interaction, frugivores improve their density equilibria by getting extra food. Using our model, we now show the animals benefit from this mutualistic interaction and compare frugivores dynamics with and without plants.

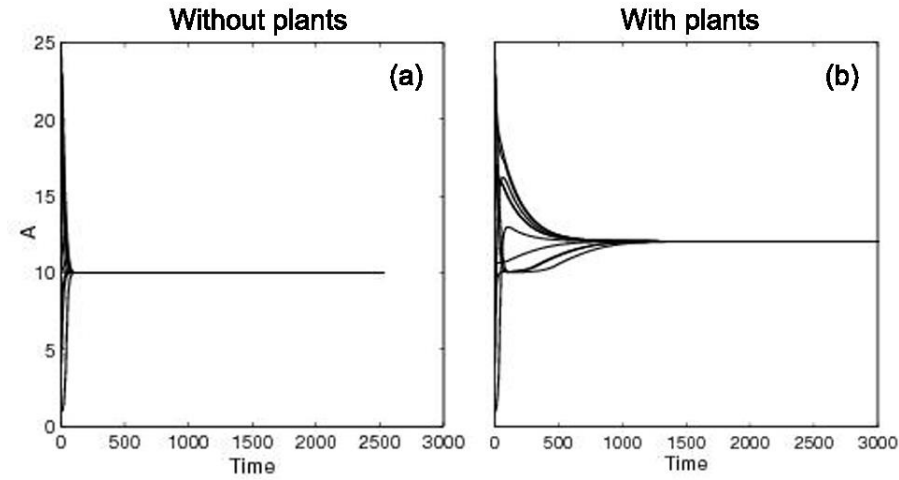


Figure 4.6: Animal dynamics without and with plants. Animal trajectories without plants (first column) and with plants (second column). All parameters at their reference values

Figure 4.6 illustrates changes in animals equilibrium in the absence and presence of plants. In the absence of plants (panel a), animals converges to a stable equilibrium ($K = 10$) which represents their carrying capacity in our model. There is a obvious support from plants to animals (compare panel a with b) due to the interaction and the benefit gained from the fruits nutrition.

Results that are presented in this chapter show the benefits for both plants and animals for plant-frugivore mutualistic interaction. Frugivorous animals influence plant persistence and changes plant spatial distribution. While animals increase their density equilibria by consuming fruits pulp of plants.

Chapter 5

Discussion

By proposing a novel pair approximation model for the plant-animal mutualistic interaction, we have demonstrated that seed dispersal by animals can reduce intraspecific competition between plants and is a crucial ecological process for the persistence of plants (Figure 4.2). Not only can it increase plant global density (Figure 4.1), but also the chance for the plant to (conditionally) persist in otherwise poor habitat quality (Figure 4.2 b and d). Our theoretical findings complement empirical studies, confirming the importance of plant-frugivore interactions for successful plant recruitment, forest restoration and the provision of ecosystem functioning (e.g., da Silva et al. 2015, Archer and Pyke 1991, Caughling et al. 2015). In particular, we argue that our results could be more significant in tropical regions where most plants rely on frugivores to disperse their seeds (Howe 1984, Schleuning et al. 2011, Chama et al. 2013). However, for a plant-frugivore interaction to be fully beneficial to the plant, the frugivore must necessarily be an efficient seed disperser with low risks associated with dispersal (Figure 4.3a) and sufficient fruit consumptions (Figure 4.3b). Otherwise, frugivorous animals might act as a main driver of plant extinction by behaving as seed-predators (Figure 4.4b ; Janzen 1970, 1971, Jordano 2002).

In addition to the crucial role of seed-dispersal in plant persistence and population dynamics, it also changes the spatial distribution of plants (Figure 4.1 ; also see Nathan & Muller-Landau 2000, Beckman et al. 2012). Indeed, plant-frugivore interaction can facilitate plants to shift their niches due to climate change (Archer and Pyke 1991). Furthermore, Jordano (2000) argued that fruits are extremely aggregated in space, relative to other food resources, with high local abundance. Such a high level of clustering has been shown in our results to become mitigated in the presence of frugivores (Figure 4.1e). Such changes in plant spatial distribution could then affect the reproduction and recruitment of plants (Beckman and Rogers 2013). With seed dispersal, plant spatial distribution can be also imprinted by the spatial distribution of their dispersal agents (Nathan & Muller-Landau 2000). In our model, we assume

that the distribution of frugivores and their foraging behaviour are random. Affected by the spatial distribution of their dispersal agents, dispersed seeds in our model also tend to become randomly distributed in space (Figure 4.1f and Figure 4.2b). Efficient frugivores can thus reduce plant clustering by increasing global over local dispersal (Figure 4.1e and f).

Introduction of seed-dispersal agents allows the plant dynamics to display the scenario of conditional persistence. Efficient frugivores can maintain plants at an alternative regime of high densities, other than extinction, provided that the initial plant density is sufficiently high to allow such extended persistence (Figure 4.1d). Hence, with respect to the conservation of an ecosystem with endangered plant populations, the introduction or augmentation of populations of animal seed-dispersers would be an efficient strategy for the plant to escape extinction. In this regard, our study confirms previous suggestions on conservation policy that aims to restore animal-dispersed tree species in tropical forests (Brodie and Aslan 2012), or to conserve the process of seed-dispersal itself in temperate ecosystems by first increasing the abundance of frugivorous birds (Garcia et al. 2010).

Notice, however, that the presence of animal seed dispersal turns the extinction-persistence transition from smooth and gradual to abrupt and catastrophic. For instance, without frugivores, the decrease in habitat quality (thus seed production rate in Figure 4.2a, b) would smoothly bring plants to low densities and gradual extinction (Figure 4.2a), but the abrupt collapse of the plant population from higher density with frugivores. Such a catastrophic transition is difficult to revert due to hysteresis in the system, implying that the habitat quality to be restored greatly exceeds the one that caused the sudden collapse. Thus, early warning signals should be monitored in the presence of animal dispersers to avoid such unwanted regime shift (Scheffer et al. 2009, Drake & Griffen 2010, Kefi et al. 2014). An easy detectable and measurable early warning signal suggested by our analysis is the plant spatial clustering, i.e., the mismatch between the local and the global density of plants (see Figure 4.2b, d and Figure 4.3). The hysteresis in such systems can also be used for the control and eradication of alien invasive plants. In such cases, the removal of animal seed dispersers (Figure 4.1 and 4.2), the decrease of plant fertility and vegetative local dispersal (Figure 4.2 and 4.4), or the inhibition of plant-animal interaction and animal dispersal efficiency (Figure 4.3 and 4.4) could all serve to achieve successful eradication.

Despite the importance of animal seed dispersers, plant persistence is firstly determined by the quality and availability of habitat. Without intervention from dispersal vectors, only those plants with high fecundity (mainly determined by a high habitat quality) and a high potential for local dispersal (determined by habitat availability) can persist (Figure 4.2a and c; Figure 4.4a). Variation

and fragmentation of habitat can influence plant fecundity and consequently plant dynamics, density and persistence (Beckman and Rogers 2013, Brudvig et al. 2015). However, not only can habitat quality affect the plant fecundity, but also can influence plant-frugivore interactions (Brudvig et al. 2015). High habitat quality increases the probability of seed recruitment (Beckman and Rogers 2013) and allows plant persistence (Figure 4.1e; Figure 4.4c and d). Conversely, low habitat quality drives plants to extinction even if their seeds are dispersed by efficient frugivores (Figure 4.1a and b; Figure 4.4a). The possibility of habitat heterogeneity (local versus global habitat quality) could further complicate the spatial and dynamical regimes of plants. Taken together, frugivore-mediated seed dispersal can influence plant persistence, abundance, and spatial distribution. It allows conditional persistence of plants with relatively low fecundity and low local dispersal ability, which cannot persist without frugivory.

Chapter 6

Conclusion, limitation and future direction

By using pair-approximation method we proposed a process-based mechanistic model of frugivorous seed-dispersal. The model considers plant-frugivore mutualistic interaction which benefits both partners. The animals benefit is quite obvious, food, and plants benefit is seed dispersal leading to reduced clustering of plants, inbreeding pressure and lessens density-dependent seed mortality near parent plants. In addition to the production rate and germination probability of seeds, we further consider two essential elements of frugivorous seed-dispersal, including the strength of plant-frugivore mutualistic interaction (characterized by frugivore attack rate and seed production rate of plants) and dispersal efficiency of frugivore. We investigated how different factors, including seed production rate, dispersal efficiency and the attack rate of frugivores as well as plant dispersal ability, alone or in combinations among them, can affect the spatial and temporal dynamics of plants.

Our results showed that frugivorous seed-dispersal is a crucial process for plant persistence, abundance and spatial distribution, especially in tropical regions where plants entirely rely on frugivores to disperse their seeds. More importantly, efficient frugivores allow conditional persistence of plants with relatively low fecundity and low dispersal ability. Our theoretical findings agreed with previous empirical studies and confirmed the positive influences of frugivores on the reduction of plants clustering and hence intraspecific competition among individual plants.

However, our model only considers the plant-frugivore global interaction with seeds dispersed globally (i.e., everywhere in the lattice). One can extend this model by considering animals local interaction within neighboring sites of focal plants (i.e., local density of plants). We can further extend our model by introducing the effects of heterogeneity and fragmentation of the landscapes on frugivorous seed-dispersal. Finally, using this model, one can apply adaptive

CHAPTER 6. CONCLUSION, LIMITATION AND FUTURE DIRECTION **37**

dynamics theory and investigate the co-evolutionary dynamics of both plants and animals phenotypic traits (e.g., fruit size of plants and mouth size of animals).

Appendices

Appendix A

Matlab codes

Below are two Matlab codes for both plants (with and without animals) and animals (with and without plants) dynamics. Notice, however, that all figures from those codes have been edited using Matlab to get the final figures presented in this thesis. Matlab continuation package (MATCONT) has also been used for doing bifurcation analysis.

Matlab code I: Trajectories of our model

The outcome of this code was presented in Figure 4.1

```
function PqA_solution()
clear all
close all

% parameter values
d = 0.07; % natural death rate of plants
a = 0.1; % frugivore attack rate
r = 1 ; % intrinsic growth rate of frugivore
k = 10; % frugivore carrying capacity
z = 2; % number of neighboring sites of a focal plant
mu = 0.8; % frugivore dispersal efficiency
alpha = 0.2; % frugivore conversion efficiency
m = 10; % seed production rate of plants
g = 0.01; % seed germination probability

% period of the solution
initialTime = 0;
endTime = 20000;
timeSpan = [initialTime, endTime];

% initial conditions1
```

```
Pinitial1 = 0.01;
Ainitial1 = 1; %1
qinitial1 = 1 ;
initialConditions1 = [Pinitial1 Ainitial1 qinitial1];
initialConditions1noA = [Pinitial1 0 qinitial1];

% initial conditions2
Pinitial2 = 0.7;
Ainitial2 = 1;
qinitial2 = 0.5714 ;
initialConditions2 = [Pinitial2 Ainitial2 qinitial2];
initialConditions2noA = [Pinitial2 0 qinitial2];

% initial conditions3
Pinitial3 = 0.01;
Ainitial3 = 1;
qinitial3 = 0 ;
initialConditions3 = [Pinitial3 Ainitial3 qinitial3];
initialConditions3noA = [Pinitial3 0 qinitial3];

% initial conditions4
Pinitial4 = 0.99;
Ainitial4 = 1;
qinitial4 = 1 ;
initialConditions4 = [Pinitial4 Ainitial4 qinitial4];
initialConditions4noA = [Pinitial4 0 qinitial4];

% initial conditions5
Pinitial5 = 0.5;
Ainitial5 = 1;
qinitial5 = 0 ;
initialConditions5 = [Pinitial5 Ainitial5 qinitial5];
initialConditions5noA = [Pinitial5 0 qinitial5];

% initial conditions6
Pinitial6 = 0.5;
Ainitial6 = 1;
qinitial6 = 1;
initialConditions6 = [Pinitial6 Ainitial6 qinitial6];
initialConditions6noA = [Pinitial6 0 qinitial6];

% initial conditions7
Pinitial7 = 0.04;
```

```
Ainitial7 = 3;
qinitial7 = 1;
initialConditions7 = [Pinitial7 Ainitial7 qinitial7];
initialConditions7noA = [Pinitial7 0 qinitial7];

% initial conditions8
Pinitial8 = 0.01;
Ainitial8 = 3;
qinitial8 = 0.4;
initialConditions8 = [Pinitial8 Ainitial8 qinitial8];
initialConditions8noA = [Pinitial8 0 qinitial8];

% initial conditions9
Pinitial9 = 0.55;
Ainitial9 = 3;
qinitial9 = 0.2;
initialConditions9 = [Pinitial9 Ainitial9 qinitial9];
initialConditions9noA = [Pinitial9 0 qinitial9];

% initial conditions10
Pinitial10 = 0.2;
Ainitial10 = 3;
qinitial10 = 0;
initialConditions10 = [Pinitial10 Ainitial10 qinitial10];
initialConditions10noA = [Pinitial10 0 qinitial10];

% initial conditions11
Pinitial11 = 0.3;
Ainitial11 = 3;
qinitial11 = 0.8;
initialConditions11 = [Pinitial11 Ainitial11 qinitial11];
initialConditions11noA = [Pinitial11 0 qinitial11];

% initial conditions12
Pinitial12 = 0.57;
Ainitial12 = 3;
qinitial12 = 0.27;
initialConditions12 = [Pinitial12 Ainitial12 qinitial12];
initialConditions12noA = [Pinitial12 0 qinitial12];

% initial conditions13
Pinitial13 = 0.05;
Ainitial13 = 3;
qinitial13 = 0.9;
```

```
initialConditions13 = [Pinitial13 Ainitial13 qinitial13];
initialConditions13noA = [Pinitial13 0 qinitial13];

% initial conditions14
Pinitial14 = 0.06;
Ainitial14 = 3;
qinitial14 = 0.9;
initialConditions14 = [Pinitial14 Ainitial14 qinitial14];
initialConditions14noA = [Pinitial14 0 qinitial14];

% initial conditions15
Pinitial15 = 0.2;
Ainitial15 = 3;
qinitial15 = 1;
initialConditions15 = [Pinitial15 Ainitial15 qinitial15];
initialConditions15noA = [Pinitial15 0 qinitial15];

% initial conditions16
Pinitial16 = 0.3;
Ainitial16 = 3;
qinitial16 = 0;
initialConditions16 = [Pinitial16 Ainitial16 qinitial16];
initialConditions16noA = [Pinitial16 0 qinitial16];

% initial conditions17
Pinitial17 = 0.7;
Ainitial17 = 3;
qinitial17 = 1;
initialConditions17 = [Pinitial17 Ainitial17 qinitial17];
initialConditions17noA = [Pinitial17 0 qinitial17];

% initial conditions18
Pinitial18 = 0.03;
Ainitial18 = 3;
qinitial18 = 0;
initialConditions18 = [Pinitial18 Ainitial18 qinitial18];
initialConditions18noA = [Pinitial18 0 qinitial18];

% initial conditions19
Pinitial19 = 0.04;
Ainitial19 = 3;
qinitial19 = 0;
initialConditions19 = [Pinitial19 Ainitial19 qinitial19];
```

```

initialConditions19noA = [Pinitial19 0 qinitial19];

% solutions using ode45 and plots
options = odeset('RelTol',10^-6,'AbsTol',10^-9);
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions1,options);
figure
plot(x(:,1),x(:,3))
if x(end,1)<10^-4 x(end,3)=0; end;
plot(x(end,1), x(end,3),'ko','MarkerEdgeColor','k','MarkerFaceColor','k',
'MarkerSize',8)
xlabel('P_+', 'FontSize',11);
ylabel('q_{+|+}', 'FontSize',11);
title('Trajectories of the solution with animals','FontSize',12)
axis square
box on
hold on
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions2,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions3,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions4,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions5,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions6,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions7,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions8,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions9,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions10,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions11,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions12,options);
plot(x(:,1),x(:,3))
hold on
if x(end,1)<10^-4 x(end,3)=0; end;
plot(x(end,1), x(end,3),'ko','MarkerEdgeColor','k','MarkerFaceColor','k',
'MarkerSize',8)
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions13,options);
plot(x(:,1),x(:,3))

```

```

[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions14,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions15,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions16,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions17,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions18,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions19,options);
plot(x(:,1),x(:,3))
hold off

% this is the solution of the system without animals
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions1noA,options);
figure
plot(x(:,1),x(:,3))
if x(end,1)<10^-4 x(end,3)=0; end;
plot(x(end,1), x(end,3),'ko','MarkerEdgeColor','k','MarkerFaceColor','k',
,'MarkerSize',8)
xlabel('P_+', 'FontSize',11);
ylabel('q_{+|+}', 'FontSize',11);
title('Trajectories of the solution with no animal','FontSize',12)
axis square
box on
hold on
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions2noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions3noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions4noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions5noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions6noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions7noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions8noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions9noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions10noA,options);

```



```

plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions11noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions12noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions13noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions14noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions15noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions16noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions17noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions18noA,options);
plot(x(:,1),x(:,3))
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions19noA,options);
plot(x(:,1),x(:,3))
hold off

```

% this function defines our frugivorous seed-dispersal model

```

function dPqA=dPqAsystem(t,x) % this function defines the system
    dPqA = zeros(3,1);
    P = x(1);
    A = x(2);
    q = x(3);
    dPqA(1) = -d*P + g*exp(-a*A*m*P)*(1 - q)*m*P
    + g*mu*(1 - exp(-a*A*m*P))*m*P*(1 - P);
    dPqA(2) = r*A*(1 - A/k) + alpha*(1 - exp(-a*A*m*P))*m*P;
    dPqA(3) = -d*q + g*exp(-a*A*m*P)*m*(1 - q)*(2/z - q)
    + mu*g*(1 - exp(-a*A*m*P))*m*(2*P - P*q - q)+(2*g*m/z)*(z-1)*exp(-a*A*m*P)
end

end

```

Matlab code II: Animals dynamics

The outcome of this code was presented in Figure 4.6

```

function animals_dynamics()
clc
clear all
close all

% parameter values
d = 0.07; % natural death rate of plants
a = 0.1; % frugivore attack rate
r = 1 ; % intrinsic growth rate of frugivore
k = 10; % frugivore carrying capacity
z = 2; % number of neighboring sites of a focal plant
mu = 0.8; % frugivore dispersal efficiency
alpha = 0.2; % frugivore conversion efficiency
m = 10; % seed production rate of plants
g = 0.01; % seed germination probability

% period of the solution
initialTime = 0;
endTime = 2000;
timeSpan = [initialTime, endTime];

% initial conditions1
Pinitial1 = 0.3;
Ainitial1 = 22; %1
qinitial1 = 1 ;
initialConditions1 = [Pinitial1 Ainitial1 qinitial1];
initialConditions1noP = [0 Ainitial1 qinitial1];

% initial conditions2
Pinitial2 = 0.7;
Ainitial2 = 25;
qinitial2 = 0.5714 ;
initialConditions2 = [Pinitial2 Ainitial2 qinitial2];
initialConditions2noP = [0 Ainitial2 qinitial2];

% initial conditions3
Pinitial3 = 0.1;
Ainitial3 = 23;
qinitial3 = 0 ;
initialConditions3 = [Pinitial3 Ainitial3 qinitial3];
initialConditions3noP = [0 Ainitial3 qinitial3];

% initial conditions4

```

```
Pinitial4 = 0.9;
Ainitial4 = 20;
qinitial4 = 1 ;
initialConditions4 = [Pinitial4 Ainitial4 qinitial4];
initialConditions4noP = [0 Ainitial4 qinitial4];

% initial conditions5
Pinitial5 = 0.85;
Ainitial5 = 17;
qinitial5 = 0.1 ;
initialConditions5 = [Pinitial5 Ainitial5 qinitial5];
initialConditions5noP = [0 Ainitial5 qinitial5];

% initial conditions6
Pinitial6 = 0.6;
Ainitial6 = 14;
qinitial6 = 1;
initialConditions6 = [Pinitial6 Ainitial6 qinitial6];
initialConditions6noP = [0 Ainitial6 qinitial6];

% initial conditions7
Pinitial7 = 0.75;
Ainitial7 = 11;
qinitial7 = 1;
initialConditions7 = [Pinitial7 Ainitial7 qinitial7];
initialConditions7noP = [0 Ainitial7 qinitial7];

% initial conditions8
Pinitial8 = 0.65;
Ainitial8 = 7;
qinitial8 = 0.4;
initialConditions8 = [Pinitial8 Ainitial8 qinitial8];
initialConditions8noP = [0 Ainitial8 qinitial8];

% initial conditions9
Pinitial9 = 0.35;
Ainitial9 = 4;
qinitial9 = 0.2;
initialConditions9 = [Pinitial9 Ainitial9 qinitial9];
initialConditions9noP = [0 Ainitial9 qinitial9];

% initial conditions10
Pinitial10 = 0.2;
Ainitial10 = 1;
```

```

qinitial10 = 0;
initialConditions10 = [Pinitial10 Ainitial10 qinitial10];
initialConditions10noP = [0 Ainitial10 qinitial10];

% solutions using ode45 and plots
options = odeset('RelTol',10^-6,'AbsTol',10^-9);
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions1,options);
figure
plot(x(:,2),'k')
xlabel('Time','FontSize',11);
ylabel('A','FontSize',11);
title('Animals dynamics with plants','FontSize',12)
axis square
box on
hold on
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions2,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions3,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions4,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions5,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions6,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions7,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions8,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions9,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions10,options);
plot(x(:,2),'k')
hold off

[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions1noP,options);
figure
plot(x(:,2),'k')
xlabel('Time','FontSize',11);
ylabel('A','FontSize',11);
title('Animals dynamics without plants','FontSize',12)
axis square
box on
hold on

```

```

[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions2noP,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions3noP,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions4noP,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions5noP,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions6noP,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions7noP,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions8noP,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions9noP,options);
plot(x(:,2),'k')
[t,x] = ode45(@dPqAsystem,timeSpan,initialConditions10noP,options);
plot(x(:,2),'k')
hold off

```

```

% this function defines the system

```

```

function dPqA=dPqAsystem(t,x)

```

```

    dPqA = zeros(3,1);

```

```

    P = x(1);

```

```

    A = x(2);

```

```

    q = x(3);

```

```

    dPqA(1) = -d*P + g*exp(-a*A*m*P)*(1 - q)*m*P
    + g*mu*(1 - exp(-a*A*m*P))*m*P*(1 - P);

```

```

    dPqA(2) = r*A*(1 - A/k) + alpha*(1 - exp(-a*A*m*P))*m*P;

```

```

    dPqA(3) = -d*q + g*exp(-a*A*m*P)*m*(1 - q)*(2/z - q)

```

```

    + mu*g*(1 - exp(-a*A*m*P))*m*(2*P - P*q - q)+(2*g*m/z)*(z-1)*exp(-a*A*m*P)

```

```

end

```

```

end

```

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